LIFE CYCLE OF AN AUSTRALIAN GLOW-WORM *ARACHNOCAMPA FLAVA* HARRISON (DIPTERA: KEROPLATIDAE: ARACHNOCAMPINAE)

C.H. BAKER and D.J. MERRITT

Department of Zoology and Entomology, School of Life Sciences, The University of Queensland, St Lucia, Qld 4072; email: c.baker1@mailbox.uq.edu.au

Abstract

The life cycle of the southeast Queensland glow-worm *Arachnocampa flava* Harrison is documented and comparisons made with the more extensively studied New Zealand glow-worm, *A. luminosa* (Skuse). The adult life span of *A. flava* is short. Females live a maximum of 2.5 days and males 6 days. Egg development time is 7-9 days and the pupal stage lasts 6-7 days. Behaviour associated with snare construction, prey capture and snare mending is described. Pupae lie suspended horizontally by an anterior and posterior bracing cord, whereas *A. luminosa* pupae are suspended vertically by a single cord attached at the thorax. Only larvae and one early stage female pupa of *A. flava* were observed to bioluminesce in the laboratory.

Introduction

Glow-worms are the bioluminescent larvae of flies from the family Keroplatidae, subfamily Arachnocampinae (Matile 1981). Larvae construct a mucous tube from which they hang a snare of silk and mucus to capture prey attracted by the larva's bioluminescence (Richards 1960). Larvae are generally long-lived while the adults are very short-lived, dying within a few days of eclosion (Richards 1960). The genus *Arachnocampa* Edwards comprises four described species, three of which are endemic to Australia (Harrison 1966). The Australian species are: *A. flava* Harrison, inhabiting rainforest areas of southeast Queensland (Perkins 1935, Harrison 1966); *A. richardsae* Harrison identified from the Newnes railway tunnel, NSW (Harrison 1966); and *A. tasmaniensis* Ferguson from Tasmania (Ferguson 1925). The fourth species, *A. luminosa* (Skuse), is endemic to New Zealand. Glow-worms have been documented from other locations within Australia (McKeown 1935, Harrison 1966, Crosby 1978, Anonymous 1994), but no taxonomic work has followed these discoveries. A review of the taxonomic history of *A. luminosa* was presented by Pugsley (1983).

In New Zealand, bioluminescent *A. luminosa* larvae have been a popular tourist attraction for many years. Consequently, a number of biological and ecological studies have focused on this species (Norris 1894, Hudson 1950, Richards 1960, Gatenby 1960a, Stringer 1967, Kermode 1974, Pugsley 1980, 1984, Meyer-Rochow 1990, Smith 1992, Broadley 1998). Pugsley's (1984) study of *A. luminosa* biology was prompted by a serious population decline between 1975 and 1980 resulting in temporary closure of Waitomo cave and considerable economic loss to the tourism industry. In Australia, a large colony of *A. flava* at Natural Bridge in Springbrook National Park, southeastern Queensland (part of the World Heritage listed Central Eastern Rainforest Reserves) is the subject of increasing tourism pressures, with an estimated 300,000 visitors per annum (Anonymous 1999). However, little is

known about the species, with the only published records of *A. flava* being an acknowledgement of a colony in Queensland (Perkins 1935) and a brief morphological description (Harrison 1966).

Sustainable glow-worm ecotourism can be promoted by providing biological information to educate tourists. Further, information on the insect's life cycle and environmental requirements is crucial for tourism management. This study was carried out to provide such information for tour operators and park managers.

Materials and methods

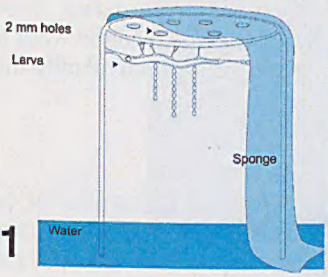
Specimen collection

Arachnocampa flava larvae and pupae were collected from Twin Falls, Springbrook National Park, Qld. Larvae moved quickly into crevices in the banks when disturbed, so their direction of movement was determined before scooping the larvae up, with fine forceps, in their snare. Pupae were collected by cutting the suspensory threads from the substrate. Both larvae and pupae were transported to the laboratory in sealed tubes to prevent desiccation.

Maintenance of cultures

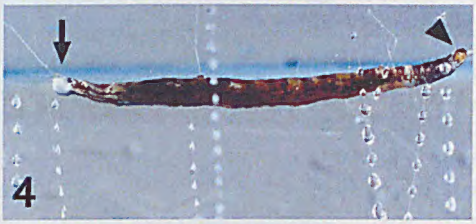
Glow-worm larvae require moist conditions for survival, thus pupae were placed on damp cotton wool within sealed jars. Individual larvae were placed in 10 cm high x 6 cm wide cylindrical, clear plastic containers inverted in 2 cm of water (Fig. 1). Holes (2 mm diameter) were drilled into the top of each container and a 20 cm piece of absorbent material was draped over the top, with one end in the water to act as a wick. Water droplets formed at the top of the container, simulating the seepage conditions occurring in the natural habitat of the glow-worms. Containers were placed in a Contherm Phototron Climate Simulator incubator at 23 ± 2°C and 98 ± 2% relative humidity.

Figs 1-6. *Arachnocampa flava*. (1) Diagram of a rearing container (10 cm high x 6 cm diameter); larvae were placed on the side of the container, from where they moved to the top and constructed a snare; containers were kept in an environment controlled incubator at 23 ± 2°C, 98 ± 2% RH. (2) Eggs and first instar larvae in laboratory culture (egg diameter = 0.4 mm, larvae 2-4 mm long); the cotton wool was kept moist to ensure eggs and emerging larvae did not desiccate. (3) Schematic diagram of a larva turning in its mucous tube: (a) - larva lies inside its mucous tube facing right; (b) - larva bites through the mucous tube with its mandibles; (c) - larva slides back along the length of its body with its anterior end on the outside of the mucous tube; (d) - larva bites through the tube again and re-enters the tube; (e) - larva is now facing left. (4) Larva (3 cm long) suspended from the substrate via bracing cords; the terminal bioluminescent region is indicated with an arrow and the sclerotised head capsule by an arrowhead. (5) Larval snare (~5 cm long); snares are a combination of bracing cords (small arrows) that suspend the snare, the mucous tube in which the larva lies, and fishing lines let down by the larva to capture small arthropods attracted to their bioluminescence. (6) Larval head capsule showing labrum (l), mandibles (m), maxilla (ma) and antennal stubs (a). Scale bar = 100 μm.


2 mm holes
Larva
Sponge
Water

1

2



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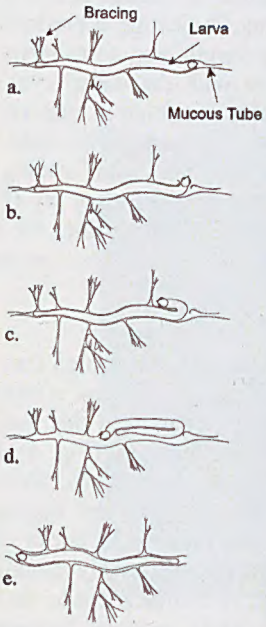
Bracing
Larva
Mucous Tube
a.
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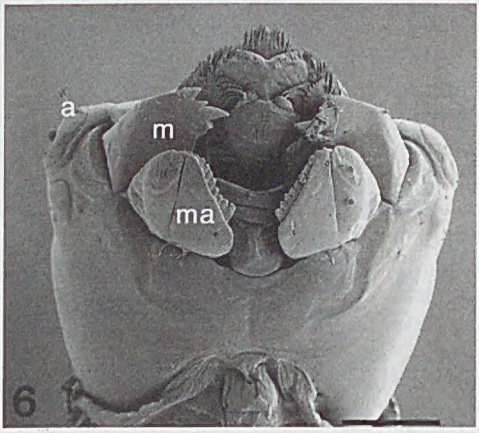
3


a
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6

Larvae were fed two to four *Drosophila melanogaster* adults per week. *Drosophila* were bred in culture on an artificial diet. *Drosophila* were anaesthetised with carbon dioxide before being placed in the larval snares. Emergent adult *A. flava* were placed in sealed jars with damp cotton wool for mating and oviposition. First instar larvae were placed individually into containers upon emergence.

Results

Eggs

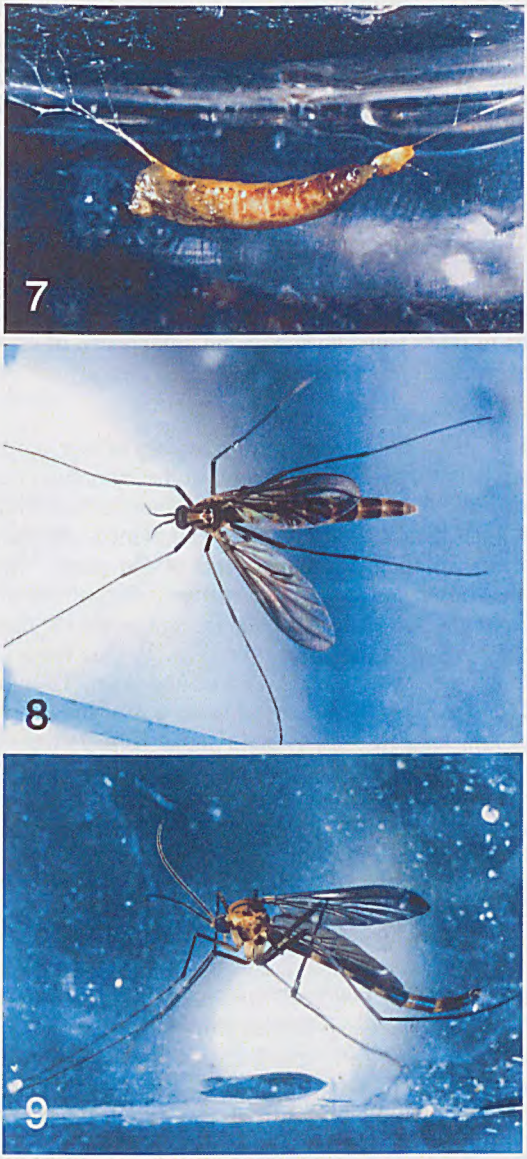
The *A. flava* egg incubation period was 7-9 days at 23°C (number of egg batches = 12). Adult females deposited an average of 129 eggs with a range of 95-164 eggs per female. The eggs (Fig. 2) stuck readily to the substrate. The eggs were orange-cream in colour when deposited and darkened over time. The empty shell is a dark red-brown after larval emergence. Eggs were 0.4 mm in diameter. Bioluminescence was not observed in the egg stage.

Larvae

The duration of the larval stage was not recorded in this study. However, in the wild there was a notable increase in the number of pupae, adults and first instar larvae during late winter and early spring, indicating a predominantly annual cycle. First instars were 2-4 mm in length and transparent upon emergence (Fig. 2). They were difficult to see with the naked eye, except when bioluminescing. Early instar larval mortality was high in captivity, with no larvae progressing to the third instar. Newly hatched or relocated larvae immediately suspended themselves from the substrate with bracing cords attached from the substrate to the mucous tubes in which they lay (Fig. 3). First instar larvae in culture did not construct vertical fishing lines for at least seven days after emergence. First instars moulted after 21 days. Larvae were 3-4 cm long at pupation.

Larval behaviour

Larvae spent much of their time inside their mucous tubes, which they broke through to repair their snares, feed and to turn around. To turn, a larva bites through the mucous tube and slides back against its body head first, before re-entering the tube further down, facing the opposite direction (Fig. 4). Larvae devoted a significant amount of time to maintaining their snares. We use the term snares to encompass the mucous tube, bracing lines and fishing lines (Fig. 5). Fishing lines consist of silk threads with a series of sticky mucous droplets. The silk lines and mucous droplets were presumably produced by the larva's salivary glands. The larva pulled the silk threads out to its labrum (Fig. 6) by moving its mandibles constantly. Sticky mucous droplets were attached to the silk with the larvae still moving its mandibles and its head and body in a nodding motion. Tangled fishing lines were severed by the larva's mandibles either at the fishing line attachment point or closer to the entanglement. Fishing lines with remains of older prey items or faecal particles were discarded this way.



Figs 7-9. *Arachnocampa flava*. (7) Female pupa (12 mm long) suspended horizontally with two bracing threads; bracing threads are attached to the thorax and the distal end of the abdomen. (8) Adult female (10 mm long) reared from a laboratory cultured larva. (9) Adult male (9 mm long) reared from a laboratory cultured larva.

Bracing threads were added to the snare by touching the substrate with the distal tip of the labrum to stick a thread to the substrate. The larva then released a silk line from its continuously moving mandibles and attached the opposite end to its mucous tube in which it lay. Prey items caught in the fishing lines were pulled up with the larva's mandibles repeatedly grabbing the thread on which the prey was stuck and attaching it to its mucous tube. Mucous droplets engulfed the larva's head as the lines were hauled up although the droplets quickly disappeared, presumably through the larva consuming the fluid. This way, the larva was able to quickly haul the prey item up to the mucous tube to begin feeding. The larvae attached many bracing threads to prey items, thus stopping any chance of escape. *Drosophila* fed to laboratory reared glow-worms were eaten entirely.

Pupae

Adults are difficult to find in nature hence one of our aims was to collect larvae and rear them through to adulthood in the laboratory. Larvae that were about to pupate removed many of the fishing lines in their immediate vicinity. They became quiescent and progressively shortened. At pupation the larval exuvium was pushed to the posterior end of the pupa, where it remained attached to the posterior suspensory thread. Pupae remained suspended horizontally from the substrate via anterior and posterior threads, consisting of the dried remnants of the mucous tube (Fig. 7). One thread was attached to the thorax and the other to the distal end of abdomen. The pupal stage lasted 6-7 days at 23°C (n = 14). Male pupae were 9 mm long (n = 8) and female pupae were 12 mm long (n = 6). Female pupae (Fig. 7) were recognisable by their swollen abdomen relative to males. Only one early stage female pupa was observed to bioluminesce and could occasionally be induced to glow by lightly tapping its container. Pupal bioluminescence was observed as a short burst of bright light similar in intensity to larval bioluminescence. The pupa doused its light within seconds of being disturbed by vibrations or artificial light.

Adults

Adults emerged from the pupal case head first. They frequently remained partly contained in the pupal case or suspended upside down for up to a day, although they would fly away if disturbed. Female *A. flava* (Fig. 8) lived a maximum of 2.5 days (n = 20) and males (Fig. 9) lived for 6 days when unmated and 4 days when mated (n = 13). Females were 6.5-10 mm long (n = 25) and males 6.5-8 mm (n = 17) (Table 1). Neither sex was observed to bioluminesce at any time. Male adults were more active fliers than females, whose abdomens were swollen with eggs.

Mating usually took place immediately upon female emergence if adult males were placed in containers with female pupae, but took longer to initiate if they were placed together as adults. Males were able to mate with different females numerous times (four viable egg batches from one male), while

females mated once and began ovipositing. Copulation duration varied, with recorded matings lasting from one hour to greater than seven hours (n = 8). Onset and duration of oviposition was also variable with some females beginning oviposition immediately following copulation. Eggs were deposited onto damp cotton wool placed in the containers to elevate humidity. No sign of adult feeding was observed.

Table 1. Comparison of adult body and wing sizes between *Arachnocampa flava* and *A. luminosa**.

		Male		Female	
		Body	Wing	Body	Wing
A. flava (bush)	Mean	7.74mm	5.06mm	7.9mm	5.44mm
	Range	6.5-8mm	4.5-6mm	6.5-10mm	4.75-7mm
	S.D.	0.79	0.53	1.07	0.62
	Number	17	17	25	25
A. luminosa (cave)	Mean	13.3mm	7.9mm	14mm	10.2mm
	Range	12-15mm	7-8.5mm	13-16mm	9-12mm
	S.D.	0.97	0.46	0.85	0.84
	Number	17	17	16	15
A. luminosa (bush/tunnel entrances)	Mean	10.6mm	6.5mm	11.4mm	8.2mm
	Range	9-11mm	6-7mm	10-13mm	7.5-9mm
	S.D.	0.73	0.50	1.08	0.78
	Number	9	9	12	12

*Measurements of *A. luminosa* recorded by Richards (1960).

Discussion

Eggs

Size differences were evident at all stages of development between *A. flava* and *A. luminosa.* The *A. flava* egg diameter was substantially smaller than the 0.75 mm diameter recorded for *A. luminosa* eggs (Richards 1960). The average number of eggs laid by *A. flava* females was similar to Richard's (1960) record of an average of 130 eggs laid by *A. luminosa* females. A lower estimate of 80 eggs per *A. luminosa* female (Gatenby 1960a), was based on counts from dissected wild-caught females. This estimate, however, overlooked the fact that the females may have commenced laying before they were caught (Richards 1960), although Richards (1960) recorded a range of 84-170 eggs laid by females.

The eggs of *A. luminosa* were reported to hatch after 22-24 days at Waitomo Cave temperature (13.7-15.6°C) (Richards 1960). Our observations showed a much shorter egg development time for *A. flava* eggs, hatching after 7-9 days when maintained at 23°C. The difference may be a result of the lower temperatures during *A. luminosa* development, or may reflect species

differences. The lower average temperature in the Waitomo Cave system may have resulted in an extended development time for *A. luminosa*. Although differing temperatures would also explain the difference in pupation time recorded for *A. flava* and *A. luminosa* (Richards 1960), the adult life span is similar for both species, suggesting either the differing developmental times during the egg and pupal periods are species differences, or the adult stage is not affected by differing temperatures.

Larvae

Observations of larval behaviour revealed many similarities in snare maintenance and prey capture between *A. flava* and *A. luminosa* (Hudson 1950, Richards 1960, Gatenby and Cotton 1960, Richards 1963, Stringer 1967). Because of the difficulty of tracking individual larvae in the field and their relatively slow developmental rate, the precise duration of the larval stage of both species remains unknown (Richards 1960, Pugsley 1980), although estimates range from 5 to 12 months depending on environmental conditions and prey availability (Richards 1960, Pugsley 1980, personal observations).

Pupae

We found larvae and female pupae to be the only bioluminescent stages in *A. flava*. By comparison, larvae, pupae and adults of *A. luminosa* are reported to bioluminesce by some authors (Richards 1960, 1963, Kermode 1974, Meyer-Rochow and Waldvogel 1979). Observations differ as to whether pupal and adult male *A. luminosa* bioluminesce. In *A. luminosa* degeneration of light organs during pupation has been reported (Gatenby 1959, 1960a, 1960b), although male pupae and adults have been reported to bioluminesce in the field (Richards 1960, 1963, Vandel 1965, Kermode 1974). *A. flava* male pupae and adults do not bioluminesce. Dissections of the pupal and adult light organs of *A. flava* may reveal whether the male bioluminescent organs degenerate during pupation.

The role of bioluminescence in mate attraction in *Arachnocampa* remains controversial (Gatenby 1959, Richards 1960, Crosby 1978). In both *A. luminosa* and *A. flava*, adult males are commonly seen suspended from female pupae, apparently waiting for females to eclose, whereupon they copulate (Richards 1960, personal observations). It has been suggested that pupal bioluminescence is an attractant for mates (Richards 1960) but there has been no experimental confirmation. We found copulation consistently occurred sooner when male and female *A. flava* pupae were put together as opposed to adults. Males in containers with a female pupa wait near the female pupa, suggesting that copulation at female eclosion is the norm in *A. flava*, however field observations are required to confirm this. Males could be attracted to pheromones originating from the female pupa or to the short bursts of bright female pupal light.

An obvious difference between *A. luminosa* and *A. flava* is the method of pupal suspension. Pupae of *A. flava, A. richardsae and A. tasmaniensis* (*A. tasmaniensis* is included in the same subgenus as *A. luminosa*) suspend themselves horizontally rather than vertically as is the case for *A. luminosa* (Richards 1960). The single strand suspension of *A. luminosa* may reduce predation or facilitate mate attraction. The two strand suspension of *A. flava* may enable the pupa to withstand more turbulent wind conditions by reducing movement of the pupa and the possibility of entanglement in its remaining snares.

Adults

The adult life span of *A. flava* is similar to that recorded for *A. luminosa.* Size differences are evident between *A. flava* and *A. luminosa* with *A. luminosa* the larger of the two (Table 1). It has been noted that adult New Zealand glow-worms from caves are larger than epigean individuals, attributed to an increased food supply within the cave systems (Richards 1960, Pugsley 1980). More suitable climatic factors within caves were also suggested as a factor leading to increased body size (Pugsley 1980). The size difference between *A. flava* (bush) and *A. luminosa* (cave and bush types) may be attributed to species differences.

Copulation was observed to decrease the lifespan of adult male *A. flava* by as much as two days. This shortening of life expectancy has not been investigated in *A. luminosa.* Perhaps the energy expenditure associated with copulation reduces male life span. *Arachnocampa* adults have not been observed to feed and are reported to possess vestigial mouthparts (Meyer-Rochow 1990).

Mated *Arachnocampa* females have been observed ovipositing on both artificial and natural sites (Richards 1960, personal observations). Female *A. flava* oviposited on damp cotton wool in the laboratory and *A. luminosa* females oviposited on quadrat markers and light fittings in the Waitomo Caves (Richards 1960). In the wild, female *A. luminosa* (Richards 1960) and *A. flava* (personal observations) have been observed to oviposit on the fringes of existing colonies. The gravid adult female *Arachnocampa* are weak fliers (Richards 1960, Meyer-Rochow 1990) which may also restrict their ability to colonise new areas. The singular and regular distribution of eggs by ovipositing females may reduce cannibalism in the early instars as the larvae are territorial and readily feed on each other if crowded (Gatenby 1959, Broadley 1998, personal observation).

The short adult life span of *A. flava*, the low mobility of adults and the tendency of females to deposit eggs on the edge of existing colonies has implications for management of colonies of tourism significance. In the event of a disastrous colony decline, regeneration could be slow if reliant on natural recolonisation. Contingency plans based on translocation of larvae from other

colonies could enhance recovery. Methods for collecting, transporting and maintaining larvae in captivity have now been developed. Information gained in this study will also be useful for increasing tourist awareness of the biology of *A. flava* and has been incorporated into interpretive material displayed at Natural Bridge, Springbrook National Park, Queensland.

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References

ANONYMOUS. 1994. *Melba Gully State Park draft management plan.* Department of Conservation and Natural Resources, Victoria, southwest Area; 21 pp.

ANONYMOUS. 1999. *Visitor information, Natural Bridge section, Springbrook National Park.* Queensland Parks and Wildlife Service, Brisbane; 2 pp.

BROADLEY, R.A. 1998. *Behavioural ecology and prey attraction of the New Zealand glowworm* Arachnocampa luminosa *(Skuse) (Diptera: Mycetophilidae) in bush and cave habitats.* Unpublished M.Sc thesis, Massey University, Aukland; 121 pp.

CROSBY, D.F. 1978. Glow-worms. *Victorian Entomologist* **8**: 56-59.

FERGUSON, E.W. 1925. Description of a new species of Mycetophilidae (Diptera) with luminous larvae. *Proceedings of the Linnean Society of New South Wales* **50**: 487-488.

GATENBY, J.B. 1959. Notes on the New Zealand glow-worm, *Bolitophila (Arachnocampa) luminosa. Transactions of the Royal Society of New Zealand* **87**: 291-314.

GATENBY, J.B. 1960a. The New Zealand glow-worm. *Tuatara* **8**: 86-92.

GATENBY, J.B. 1960b. The Australian mycetophilid glowworms. *Transactions of the Royal Society of New Zealand* **88**: 577-593.

GATENBY, J.B. and COTTON, S. 1960. Snare building and pupation in *Bolitophila luminosa. Transactions of the Royal Society of New Zealand* **88**: 149-156.

HARRISON, R.A. 1966. Australian glow-worms of the genus *Arachnocampa* Edwards. *Pacific Insects* **8**: 877-883.

HUDSON, G.V. 1950. The natural history of the New Zealand glowworm. *Fragments of New Zealand Entomology.* Ferguson and Osborne, Wellington; pp 1-30.

KERMODE, L.O. 1974. The New Zealand glowworm *Arachnocampa luminosa. New Zealand Speleological Bulletin* **5**: 313-328.

MATILE, L. 1981, Description d'un Keroplatidae du Cretace moyen et donnees morphologiques et taxonomiques sur les Mycetophiloidea (Diptera). *Annals de la Société entomologique de France* (new series) **17**: 99-123.

McKEOWN, K.C. 1935. *Insect wonders of Australia.* Angus and Robertson, Sydney; 252 pp.

MEYER-ROCHOW, V.B. 1990. *The New Zealand glowworm.* Waitomo Caves Museum Society, Waitomo; 55 pp.

MEYER-ROCHOW, V.B. and WALDVOGEL, H. 1979. Visual behaviour and the structure of dark and light-adapted larval and adult eyes of the New Zealand glowworm *Arachnocampa luminosa* (Mycetophilidae: Diptera). *Journal of Insect Physiology* **25**: 601-613.

NORRIS, A. 1894. Observations on the New Zealand glow-worm, *Bolitophila luminosa*. *Entomologists' Monthly Magazine* **30**: 202-203.

PERKINS, F.A. 1935. "Glow-worms" and other insects collected at Numimbah, Nerang Valley, Easter camp, Queensland Naturalists' Club, 1935. *Queensland Naturalist* **9**: 84-85.

PUGSLEY, C.W. 1980. *Ecology of the New Zealand glowworm in caves at Waitomo*. Unpublished Ph.D thesis, Aukland University, Aukland; 107 pp.

PUGSLEY, C.W. 1983. Literature review of the New Zealand glowworm *Arachnocampa luminosa* (Diptera: Keroplatidae) and related cave-dwelling Diptera. *New Zealand Entomologist* 7(4): 419-424.

PUGSLEY, C.W. 1984. Ecology of the New Zealand glowworm *Arachnocampa luminosa* (Diptera: Keroplatidae), in the glowworm cave, Waitomo. *Journal of the Royal Society of New Zealand* **14**: 387-407.

RICHARDS, A.M. 1960. Observations on the New Zealand glow-worm *Arachnocampa luminosa* (Skuse) 1890. *Transactions of the Royal Society of New Zealand* **88**: 559-574.

RICHARDS, A.M. 1963. Glow-worms. *New Zealand Natural History* **2**: 433-436.

SMITH, D.W. 1992. *All about ... glowworms*. Waitomo Caves Museum Society, Waitomo; 4 pp.

STRINGER, I.A.N. 1967. The larval behaviour of the New Zealand glow-worm *Arachnocampa luminosa*. *Tane* **13**: 107-117.

VANDEL, A. 1965. *Biospeleology: the biology of cavernicolous animals*. Pergamon Press, Oxford; 524 pp.